

ASCOTHORACIDA (CRUSTACEA: MAXILLOPODA) PARASITIC ON *CHRYSOGORGIA* (GORGONACEA) IN THE PACIFIC AND WESTERN ATLANTIC

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ABSTRACT

Seven new species in two genera (one new) of bathyal, gorgonian-infesting ascothoracid crustaceans are described: *Isidascus longispinatus* new species on *Chrysogorgia* cf. *elegans* north of the Bahamas; *Thalassomembracis conquistador* new genus and species on *Chrysogorgia* sp. in the Moluccas; *T. tetraedos* new genus and species on *C. papillosa* in the Macassar Strait; *T. bilobus* new genus and species on *C. cf. papillosa* from Hawaii; *T. orientalis* new genus and species on *Chrysogorgia* sp. from the Philippines; *T. acanthosphaericus* new genus and species on same host specimen as *I. longispinatus*; *T. bayeri* new genus and species on *C. desbonni* in the Yucatan Channel. All species are represented by at least one mature female; a putative male is described of *T. conquistador*, and also nauplii of *I. longispinatus*, *T. conquistador*, and *T. acanthosphaericus*. *Isidascus* and *Thalassomembracis* are closely related to *Gorgonolaureus* Utinomi, and like that genus are classified in the Synagogidae. Most of the new species are attached to their host's axis by single or paired, anterior protrusions of the sometimes bizarrely shaped carapace, and, except for a posteroventral opening, are covered over with host coenenchyme. *Thalassomembracis* species have small, grapnel-like projections over parts of their carapaces; the four Pacific species may form a monophyletic unit within the genus. *I. longispinatus* and *T. bilobus* are often infested with cryptoniscid isopods, and *T. tetraedos* shares its host with an endoparasitic pycnogonid.

Wagin's (1976) monograph on the Ascothoracida, an invaluable summary of almost everything known up till then about these crustacean parasites of anthozoans and echinoderms, lists nine genera in the subclass. In the last couple of years interest in the Ascothoracida has resurged, and four additional genera have been added (Warén, 1981; Moyse, 1983; Grygier, 1983b, c). Grygier (1981b) summarized what little was known about octocoral-infesting ascothoracids, and Moyse (1983) has added important new information. Three gorgonian-infesting species are now known. *Gorgonolaureus bikiniensis* Utinomi and *G. muzikae* Grygier live, respectively, on *Paracis squamata* (Nutting) at Bikini Atoll, and on an undescribed paramuriceid gorgonian (ident. as *Placogorgia* sp. by K. Muzik and as *?Astromuricea* sp. by F. M. Bayer) off Oahu, Hawaiian Islands. Both are bathyal species. Utinomi (1962) placed *Gorgonolaureus* in the Lauridae. Grygier (1981c) showed that this assignment was based on misinterpretations of the animal's morphology and transferred it to the Synagogidae. Moyse (1983) described a representative of a second genus, *Isidascus bassindalei*, which lives in cysts on *Acanella arbuscula* (Johnson) found on the continental slope (about 2,000 m) in the Bay of Biscay. The seven new species of ascothoracids described in the present report include a second species of *Isidascus* and six species in a new genus, *Thalassomembracis*, all parasites of the holaxonian gorgonian *Chrysogorgia*.

METHODS

All the animals described here were obtained on loan from the U.S. National Museum of Natural History. Parts of dissected individuals were mounted unstained in glycerine jelly. Some small specimens were examined whole in lactic acid. Drawings were done with the aid of cameras lucida on a Wild M5 dissecting microscope and on a Wild M20 compound microscope.

TAXONOMY

Class Maxillopoda Dahl, 1956

(definition of Grygier, 1983a)

Subclass Ascothoracida Lacaze-Duthiers, 1880

(definition of Wagin, 1976)

Order *incertae sedis*

Wagin (1976) proposed two new suborders of Ascothoracida (orders in the present classification). Lauroidida included only anthozoan parasites, and Synagogoidida included just echinoderm parasites except for *Synagoga mira* Norman which lives on an antipatharian. Because the family Synagogidae is a catch-all for primitive ascothoracids, and now includes other anthozoan parasites besides *S. mira* (Grygier, 1981c), the Synagogoidida is not well defined. Pending a complete revision of the Ascothoracida, I prefer not to use Wagin's orders.

Family SYNAGOGIDAE Gruvel, 1905

This family includes *Synagoga* Norman (parasites of anthozoans and crinoids), *Gorgonolaureus*, *Isidascus*, and *Thalassomembracis* new genus (gorgonian parasites), and *Ascothorax* Djakonov and *Parascothorax* Wagin (parasites of ophiuroids). The family needs to be revised, as mentioned above, a task beyond the scope of this paper. *Synagoga* itself is heterogeneous and is being divided into two genera (Grygier, 1983c). *Synagoga mira* is the type of its genus and family, and is apparently the closest relative to the gorgonian parasites (see Discussion). Therefore, these three genera are retained for now in the Synagogidae.

Isidascus Moyse, 1983

Diagnosis (emend. pro Moyse, 1983; ♀♀ only).—Pseudoendoparasitic on gorgonians (Octocorallia). Carapace ovoidal or spheroidal, dorsal part forming spacious brood chamber. Valves united around greater part of circumference; aperture a ventral and to varying degrees posterior slit. Tagmosis 5-6-5. Eyes absent. Antennules 6-segmented, prehensile, hirsute, 2 setae on fourth article, several on fifth; sixth article with proximal process with 3 setae and aesthetasc, long claw guard with 3 setae, and terminal claw with 3 basal setae. Antennae small, biramous. Mandibles wide basally, attenuated to needle-like distal tip, setae along posterior edge, anterior edge straight, hirsute. Maxillules broad basally, narrow distally, with parallel, ctenate rows of setae. Maxillae fused for about half of length, no posterior hooks. Medial languette large. Thoracomeres 2, 3, 4, and sometimes 5 each with tall, setose, mediodorsal horn. Pair of large, flat epaulets on sixth thoracomere. First thoracopod longer than second; long, anterodorsally directed filamentary appendage arising near its base. Rami of first and sixth limbs biarticulate. Other limbs with biarticulate exopods (second article longer than first), and shorter, triarticulate endopods (first 2 articles short, subequal). Abdomen with long penis on first segment. Telson has large posteroventral spines and blade-like furcal rami with numerous distal and medial setae.

Type-Species.—*Isidascus bassindalei* Moyse, 1983.

Remarks.—Moyse (1983) conducts an extensive comparison of *I. bassindalei* with *Gorgonolaureus* and the more primitive genus *Synagoga*. I would like to add that *Isidascus* differs from *Gorgonolaureus* in having a large filamentary appendage at the base of the first limb, somewhat larger antennules in the adult, no posterior

hooks on the maxillae (when present, the posterior prong points distally), more than one row of setae on the maxillules, and longer telsonic spines. The closest related species in *Synagoga* are *S. mira* Norman and a new species (Grygier, 1983c) which are anthozoan parasites. The other species once included in *Synagoga*, some of which are known to parasitize crinoids, are being placed in a new genus (Grygier, 1983c), and are probably not pertinent to a discussion of the origin of the gorgonian parasites. Moyse's (1983) contention that *Isidascus* and *Gorgonolaureus* evolved in parallel from different synagogid stocks is an unnecessary complication; rather, the advanced characters they (and *Thalassomembracis* new genus) have in common argue for their close affinity (see Discussion).

Isidascus longispinatus new species

Figures 1, 2

Material.—Holotype ♀ (USNM 191229) on *Chrysogorgia* sp. (USNM 52908) collected by R/V PILLSBURY, sta. P-781 (30-VII-1969; off Cabo de la Vela, Colombia, 11°30.1'N, 73°26.5'W; 531–567 m); paratype ♀ (USNM 191230) on *Chrysogorgia elegans* Verrill (USNM 50027) collected by R/V OREGON, sta. 548 (18-IV-1952; Gulf of Mexico, 27°01.4'N, 96°16.8'W; 366–512 m); paratype ♀ (USNM 191231) on *Chrysogorgia* sp. cf. *elegans* (USNM acc. no. 344508) collected by R. Carney on R/V COLUMBUS ISELEN, Cr. 8007, sta. 063 (21-X-1980; north of Bahamas, 28°06'N, 77°08'W; 1,023–1,153 m).

Relationship to Host.—The host gorgonian's coenenchyme covered the entire carapace, except for the aperture, in a thin layer. The Bahaman paratype was firmly attached upside down to the host axis at the holdfast. The other two specimens were less strongly attached, one upside down; they almost encircled the host axis above the holdfast.

Etymology.—Named for the extremely long, posteroventral telsonic spines.

Description.—Holotype 4.6 mm long, 4.3 mm high, 3.4 mm wide (Fig. 1A–C); Bahaman paratype $6.7 \times 8.7 \times 6.9$ mm (Fig. 1D); Gulf paratype $4.0 \times 4.4 \times 3.3$ mm. Carapace irregularly rounded in side view, oval in other aspects. Aperture extends along midline from anteroventral quarter to halfway up posterior side (Fig. 1B); irregularly scalloped lips interlock. Seam continues on for a short distance at posterior end of aperture. Carapace produced anteriorly into pair of lobes which may encircle axis, but do not fuse together (Fig. 1A, C). External surface of Bahaman specimen, but not others, covered with perforated, conical papillae; other pores scattered over surface in all 3 specimens. Midgut diverticula go out into carapace anterodorsal to adductor muscle; diverticula of ovaries enter body anterodorsal to gut (Fig. 1D). Dorsal part of interior of carapace serves as brood chamber.

Antennules flank and are about as long as oral cone. Antennae arise just behind basal antennular article, often hidden by adductor muscle. Front part of thorax arched, posterior end and abdomen bent into S (Fig. 1C, D). First thoracomere not well separated from head. Thoracomeres 2–4 (also 5 in Bahaman specimen) each bear tall, middorsal protrusion set with long, fine setae; longest "horn" on second segment, progressively shorter posteriorly. Ventrolateral edges of tergites obvious, produced into large, flat epaulets on sixth segment. Each thoracomere with pair of biramous, setose thoracopods not reaching as far ventrally as oral cone. Abdominal segments rectangular; first with small hump and biramous, ventral penis; third and fourth segments half as long as others; fifth (telson) with pair of enormous posteroventral spines and blade-like, setose furcal rami (Fig. 1E).

Antennules muscular, heavily armed with hairs and setae (Fig. 1F). First article with lateral hairs. Second article rectangular with anterior and posterobasal hairs.

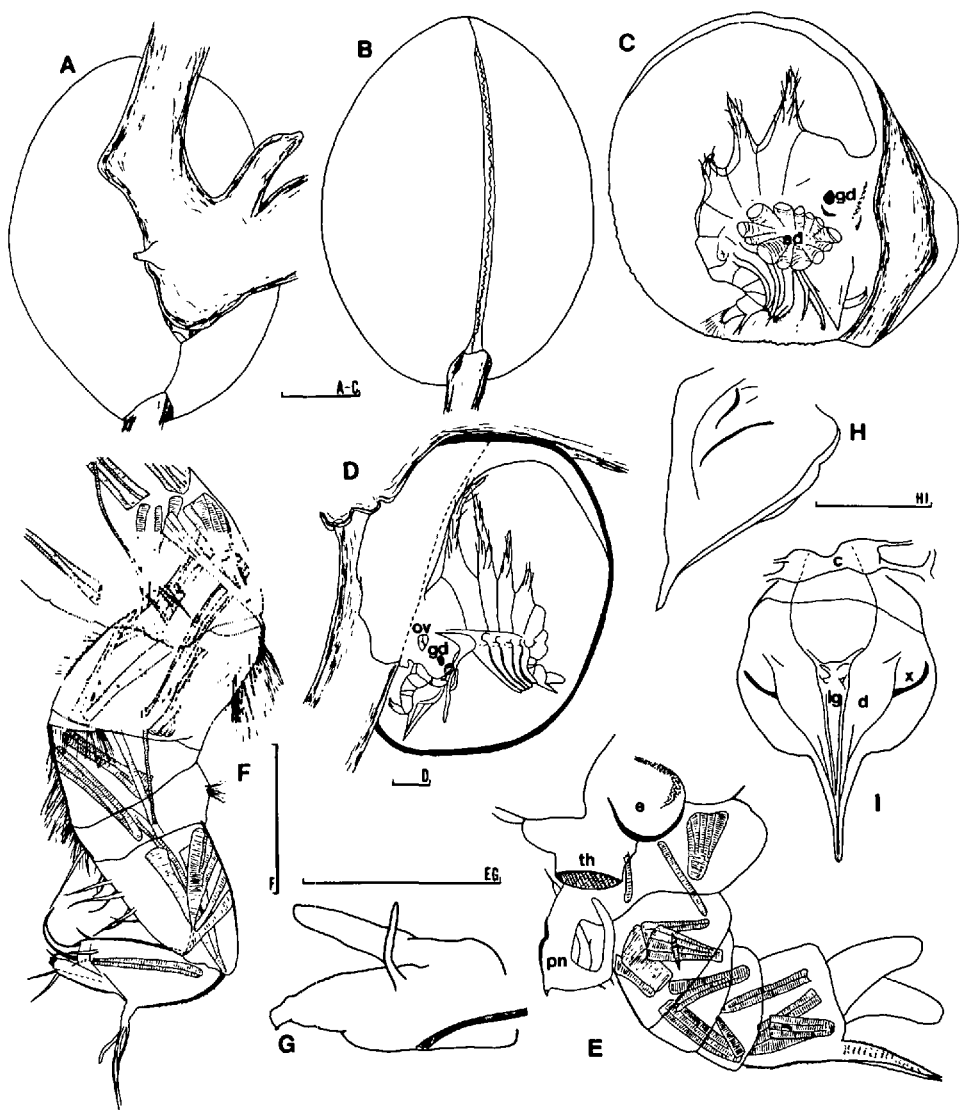


Figure 1. *Isidascus longispinatus* new genus and species: A, B, Holotype in situ on gorgonian, anterior and rear views; C, Holotype, right half of carapace removed to expose body (right antennule and antenna omitted); D, Bahaman paratype in situ, left half of carapace removed to expose body; E, Abdomen; F, Antennule; G, Antenna; H, I, Oral cone, lateral and anterior views. Scales: A-D 1.0 mm, otherwise 0.5 mm. Abbreviations: ad, adductor muscle; c, cerebral ganglion; d, mandible; e, epaulet; gd, gut diverticulum; lg, medial languette; ov, oocytes; pn, penis; th, base of sixth thoracopod; x, maxillule.

Third article triangular, half as long as second, with anterior and anterolateral hairs. Fourth article short, with anterior and posterior hairs as well as a long and short anterior seta. Fifth article tapered, with few proximal hairs and 7-12 anterior setae opposing sixth article; holotype with posterodistal hairs as well. Sixth article clasps weakly against fifth, shorter than that article; distal claw accompanied by small basal seta and larger seta on each side; cylindrical projection halfway along

posterior edge bears 3 setae and short aesthetasc; long, narrow claw guard has 2 subterminal setae, short terminal seta, and distal fringe of hairs.

Antennal rami equally long, pointing posteriorly (Fig. 1G). Ventral ramus much thicker than dorsal, and with large seta near base. Tip of dorsal ramus bifid in Bahaman specimen.

Oral cone 50% longer than deep, 30% longer than wide, triangular in side view with sharp distal point (Fig. 1H); in front view basal half bulbous, distal half very attenuated (Fig. 1I). Labrum open posteriorly. In mandibles (Fig. 2A, B), proximal third of anterior edge with hirsute sawedge, clusters of denticles giving way proximally to strong, recurved teeth. Maxillules (Fig. 2C, D) broader basally than mandibles, distal part a long, narrow triangle; medial edge straight with 2 combrows of setae along most of length except tip, and random basal hairs. Medial languette long, unarmed, triangular (Fig. 2E). Maxillae (Fig. 2F, G) extremely long and thin, tips bifid, with delicate, posterior, longitudinal flange.

First pair of thoracopods longest and of aberrant form (Fig. 2H). Whole medial edge of limb and lateral edge of exopod densely fringed with fine hairs; laterodistal coxal seta slightly longer than basis; endopod bent upward. Long, anteriorly pointing, tapered process (filamentary appendage) arises from pleural region at base of coxa.

Thoracopods 2–4 (Fig. 2I) progressively smaller posteriorly; profusely armed with fringing fine hairs and medial setae, second pair with heaviest setation. Coxa about same length as rest of limb, proximal part of lateral edge expanded into flag partly overlapping coxa behind.

Thoracopod 5 (Fig. 2J) similar to preceding 3 pairs, but lacking medial setae on coxa and basis and laterodistal coxal seta. Sixth limb smallest (Fig. 2K). Setae plumose and about same length as rami in all but exopod of first pair, where they are shorter and plainer. Setal counts for holotype and Bahaman paratype compiled in Table 1.

About half a dozen cylindrical seminal receptacles within coxae of thoracopods 2–5 (Fig. 2I, J).

Penis hanging ventrally from first abdominal segment almost reaches to third segment (Figs. 1E, 2L, M), its anterior side thickened and armed with distal spine. Few short setae on posterior side of shaft in Bahaman specimen. Short, post-spine region gives off 2 long, narrow rami with several small, scattered setae and 2 longer, terminal setae on each ramus. Rami straighter and 50% longer relative to shaft in holotype than in others (Fig. 2M), suggesting they may be erectile.

Ventrolateral corners of telson protruded into enormous spines nearly as long as furcal rami and armed with rings of spinules (Fig. 1E).

Furcal rami (Fig. 2N) bluntly tapered, downturned, basal height slightly more than half the length. Ventral half bearing cuticular ctenae; row of spines along ventral edge. Four medium-long terminal setae with short setules; 12–15 much longer setae in row along distal half of dorsal margin and diagonally to middle of medial face.

Larvae.—The holotype was brooding about 180 metanauplii. Dorsal shield vaguely kite-shaped, averaging 0.56 mm long, 0.44 mm wide (8 measured), dorsoventrally compressed (Fig. 20). Labrum small; no nauplius eye or frontal filaments observed. Antennules (Fig. 2P) unsegmented with 2 medial and at least 3 distal setae. Antennal protopods (Fig. 2Q) apparently unsegmented and unarmed, but obscured by loose cuticle; short, perhaps biarticulate endopods with mediobasal spine, 2 terminal, and 1 subterminal setae; exopods 9-segmented, last 5 articles

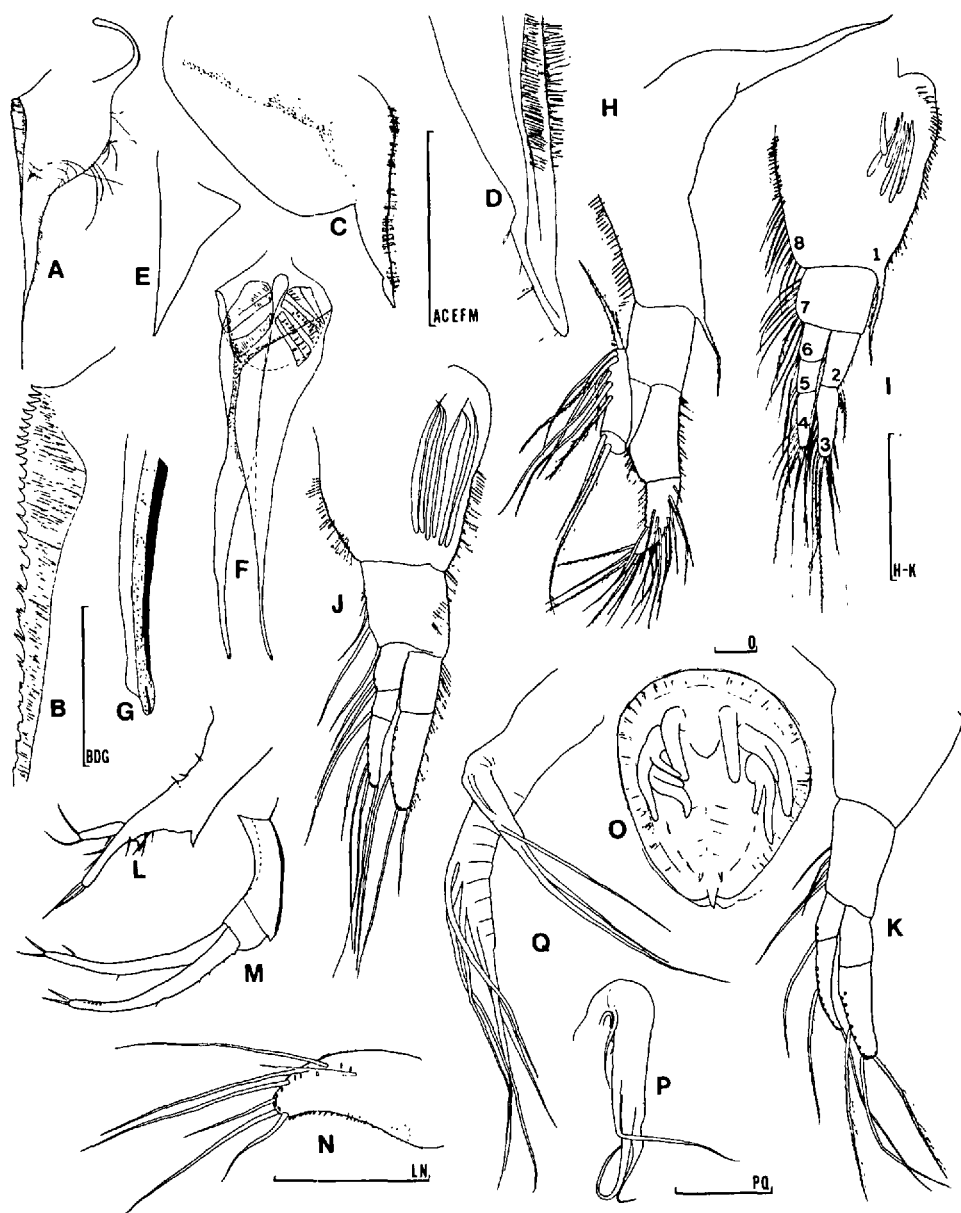


Figure 2. *Isidascus longispinatus* new genus and species: A, Mandible; B, Detail of basal part of A; C, Maxillule; D, Detail of tip of C; E, Medial languette; F, Maxillae; G, Tip of maxilla; H, First thoracopod and process at its base; I, Second thoracopod with seminal receptacles in coxa and numerals indicating sites for setal counts in Table 1; J, Fifth thoracopod with seminal receptacles in coxa; K, Sixth thoracopod; L, M, Penes of Bahaman paratype and holotype, respectively; N, Furcal ramus, medial view; O, Metanauplius, ventral view, setae omitted; P, Metanaupliar antennule; Q, Metanaupliar antenna. Only bases of many setae shown in J, K, N; only representative setulation shown on natatory setae. Scales: B, D, G, O-Q 0.1 mm, otherwise 0.5 mm.

Table 1. Thoracopodal setal counts in *Isidascus longispinatus* new genus and species. Roman numerals indicate limbs I–VI. Positions 1–8 are identified in Figure 21. Question marks indicate that the position in question was obscured. Parentheses indicate a less than usual number of rami articles, as in the first and sixth endopods. There are never any setae on the lateral side of the basis

Specimen and limbs	Position on Limb							
	1	2	3	4	5	6	7	8
Holotype, right								
I	1	0	21?	8	(2)		0?	0
II	1	1	11	6	2	2	9	12
III	1	0	12	6	3	3	8	8
IV	1	1	11	7	2	3	7	7
V	0	0	11	7	1	1	2	0
VI	0	0	8	8	(1)		2	0
Bahaman paratype, left								
I	1	0	21?	17	(5)		0?	0
II	1	1	13	10	3	5	12	12
III	1	1	15	8	3	3	12	8
IV	1	1	12	8	3	4	10	6
V	0	0	12	8	1	2	3	0
VI	0	0	13	11	(3)		4	0

with long seta. Mandibles little smaller than antennae, exopod only 6-segmented with 4 setae. Primordia of about 4 post-mandibular somites beneath cuticle. Body ends in large spine flanked ventrally by pair of small spines.

Associated Fauna.—Each paratype was host to a specimen of an undescribed species of cryptoniscid isopod (Epicaridea). *I. bassindalei* also had cryptoniscid hyperparasites (Moyse, 1983). The Bahaman specimen was attached to the same gorgonian as the holotype of *Thalassomembracis acanthosphaericus*, described below.

Remarks.—*I. longispinatus* is readily distinguished from *I. bassindalei* (Moyse, 1983). The new species is smaller. It is not found in a skeletal cup, as is the other species, and there are anterior carapace expansions for attachment. The valve aperture is longer (40 versus 30% of circumference) and more smoothly curved. The antennules of *I. bassindalei* have no posterior setae on the second article, and the posterior edges of its labrum meet posteriorly. No basal teeth are described on the mandible in *I. bassindalei*, nor bifid maxillary tips. *I. longispinatus* has no setae on the first thoracomere, and its dorsal horns are evenly, not just posteriorly, setose. The antennae are stout in *I. longispinata*, the first thoracopod has a bent endopod, and the sixth limb is no longer than the fifth, all conditions different from *I. bassindalei*. The thoracopodal setae are considerably longer in the new species, and there is no laterodistal coxal seta on the fifth limb. *I. longispinatus* has fewer setae on the terminal articles of the rami and the first endopod article of most limbs than *I. bassindalei*, but its first limb has many more setae in these locations. The penis is uniramous in *I. bassindalei*, and the furcal rami are rectangular rather than tapered, with more and shorter setae than in *I. longispinatus*. *I. bassindalei* seems to be a protandric hermaphrodite, but there is not yet evidence (besides the presence of a large penis in adult females) that this is the case in the new species.

The most striking things about *Isidascus* are the filamentary appendages at the

bases of the first limbs, and the dorsal horns. The former may be homologous with the "plate-like organs" at the base of the first limb in some species of *Baccalaureus* Broch (see Brattström, 1956). A homology with the anterior thoracic horns of *Baccalaureus* proposed by Moyse (1983) is unlikely. Most species of *Ascothorax* have similar processes that published descriptions do not explicitly mention or identify correctly, and they occur in other undescribed ascothoracids as well (Grygier, 1983). What are the filamentary appendages, and what is their function?

Pyefinch (1936) thought that the first thoracopod in *Baccalaureus* (as interpreted by Brattström, 1956) was the antenna, an imaginative interpretation that had some merit then. However, *I. longispinatus* has antennae as well as filamentary appendages, showing that these processes are not a pair of segmental limbs. Could they be epipods of the first limbs? Lack of thoracic epipods has been considered a diagnostic criterion of the Maxillopoda (Grygier, 1983a), a distinction that could be negated by the present find. Grygier (1981b) suggested that the laterodistal coxal seta might be a reduced epipod. The filamentary appendages are better candidates, except that they arise so far basally that they are not actually attached to the limb. Perhaps they are just outgrowths of the body wall with a specialized function. As the first limb moves forward and back, the process must rock up and down, with two possible results. It may impel or guide a flow of water. Or, it may push eggs dorsally into the brood chamber as they emerge from the oviduct, which is assumed to open at the base of the first limb as in other ascothoracids.

Possible functions of the dorsal horn in *Gorgonolaureus*, mostly related to water circulation and egg aeration, have been discussed earlier (Grygier, 1981b). The same explanations probably apply to *Isidascus*, but an additional possibility, suggested by the increase in number of horns with size in the new species, is that they are gas-exchange organs for the ascothoracid itself.

Thalassomembracis new genus

Diagnosis.—Carapace completely encloses main body, usually has thick, antero-ventral protrusion; valves fused except for vertical, posteroventral aperture and usually coalesced ventral seam; dorsal brood chamber elaborated into variety of species-specific shapes. Outer cuticle pierced by helical pores and produced, at least ventrally, into grapnels or radially toothed papillae. Tagmosis 5-6-5. Eyes absent. Antennules 6-segmented, weak, much shorter than oral cone when folded; 1 seta on fourth article and usually 1 on fifth (less often 2 or 0); claw guard a small, setose mound, a few other setae proximal to it. Antennae, when present, consist of short ramus and papilla. Labrum open posteriorly. Mandible wide basally, attenuated distally; setae along posterior edge; anterior edge with serrate, striated membrane that becomes frayed into twisted clumps of hairs distally, and gives way to individual hairs at tip. Maxillule triangular, usually with sparse posterodistal setae and at least 2 anterior, cteniform rows of setae. Medial languette large, tongue-shaped. Maxillae fused medially, tips bifid with posterior hooks. Setose humps on at least some thoracomeres. Pair of large, inflated epaulets on sixth thoracomere. First limb often the longest, narrower than rest, rami biarticulate. Laterodistal coxal seta in limbs 1-5, seminal receptacles in limbs 2-5. Triarticulate endopod in limbs 2-5 longer than biarticulate exopod; second endopod article very short, exopod articles equal or second one longer. Both rami biarticulate in sixth limbs. Terminal setae plumose and equal to or shorter than rami in all but first limbs, with short setules. Penis vestigial, uniramous. Telson

with rugose dorsal surface; posteroventral spines minute or absent. Furcal rami tapered, upturned, densely hirsute, with toothed scales along dorsal edge; short distal and (usually) medial setae.

Etymology.—From Greek *thalasso* (sea) and *membrax* (kind of insect), because the carapaces of some of these marine crustaceans are reminiscent of the bizarre thoraxes of treehoppers (Insecta: Homoptera: Membracidae). Gender masculine.

Type-Species.—*Thalassomembraxis conquistador* new species.

Remarks.—*Thalassomembraxis* is most closely affiliated with *Gorgonolaureus* (Grygier, 1981b, c) and *Isidascus* (cf. above, Moyse, 1983); all share a mode of life attached to and overgrown by gorgonians. All have an essentially univalved adult carapace, but the aperture is longer in the other two genera than in *Thalassomembraxis*, and they have no superficial grapnels or a medial, anteroventral anchor. The adult antennules are much less well armed and more reduced in *Thalassomembraxis* than the others. The mouthparts are similar in all three genera, but the mandibles are better armed basally in the new genus than in *Gorgonolaureus*, and the maxillae have posterior hooks, unlike *Isidascus*. The multiple rows of setae on the maxillules conform to the situation in *Isidascus*, but not *Gorgonolaureus*, which has a single row. In the other two genera, the thoracic exopods are longer than the endopods, the opposite of *Thalassomembraxis*, and their thoracopods are more setose. *G. muzikae* and *I. longispinatus* have numerous, bottle-like seminal receptacles in limbs 2–5, not just 1 or 2 like *Thalassomembraxis*, but *G. bikiniensis* has only 1. *Gorgonolaureus* has a long, curved dorsal horn on the second thoracomere, and *Isidascus* has one on several other segments as well, but neither has a horn on the first thoracomere, which is the only place anything similar is found in *Thalassomembraxis*. As far as is known, the other genera have well-developed penes, even in adult females, unlike *Thalassomembraxis*' strongly reduced penis. The tapered furcal rami with short setae of *G. bikiniensis* more closely resemble those of *Thalassomembraxis* than the broad furcal rami of *G. muzikae* or *I. bassindalei* do; the shape of the furcal rami in *I. longispinatus* is intermediate.

The hooked grapnels and other spiny devices on the carapace in *Thalassomembraxis* are reminiscent of the stellate projections scattered over the carapace in *Laura gerardiae* (Lacaze-Duthiers, 1883). Might the new genus represent an intermediate between *Gorgonolaureus* and *Isidascus*, and the zoanthid-infesting family Lauridae? *Baccalaureus*, the other genus besides *Laura* in that family, has no species with grapnels, but it shares many other derived features with *Laura* that *Thalassomembraxis* does not: an altered orientation of attachment of the body to the carapace, vestigial antennules, uniramous thoracopods filled with bulb-shaped seminal receptacles, and a 4-segmented abdomen. Therefore, either *Baccalaureus* once had grapnels and has lost them, or their appearance in *Laura* and *Thalassomembraxis* is convergent. The latter hypothesis seems more likely, because these grapnels are just modified papillae such as are found on many kinds of ascothoracids.

Thalassomembraxis conquistador new species

Figures 3, 4

Diagnosis.—Carapace about 2.5 mm, dorsal part elliptical, laterally compressed, with rounded, lateral protrusions; bifid anteroventral anchor; posterior end acute; hooked grapnels mostly ventral. Antennular claw naked, with 3 basal setae; 2 setae on claw guard, 2 on proximal process. Oral cone equilaterally triangular.

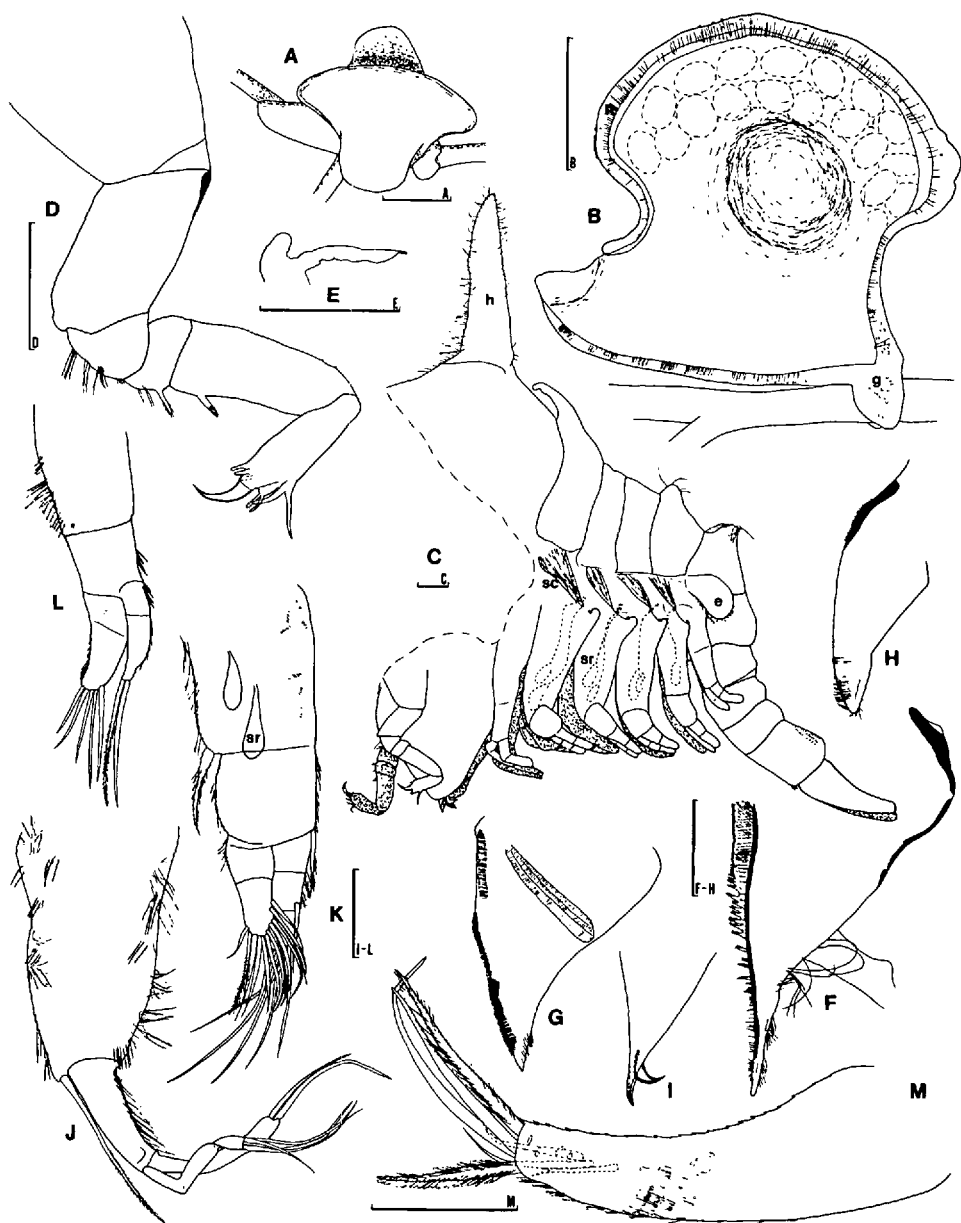


Figure 3. *Thalassomembracis conquistador* new genus and species: Paratype ♀♀. A, In situ on gorgonian, dorsal view; B, In situ, side view, showing outlines of brooding eggs; C, Main body, natatory setae omitted; D, Antennule; E, Antenna; F, Mandible; G, Maxillule; H, Medial languette; I, Tip of maxilla; J, First limb; K, Fourth limb; L, Sixth limb; M, Furcal ramus, lateral view. Only representative setulation shown in J–M, and only part of cuticular armament in M. Scales: A, B 1.0 mm, otherwise 0.1 mm. Abbreviations for Figs. 3–9: ad, adductor muscle; an, antennule; at, antenna; d, mandible; e, epaulet; g, cuticular grappels; gd, gut diverticulum; h, dorsal horn; l, maxilla; lb, labrum; ml, medial languette; oc, oral cone; p, pores; pl, polyp; sc, pleural sclerites; sp, spicules; sr, seminal receptacles; ts, testes; x, maxillule; y, yolk.

Tall, dorsal projection on first thoracomere; thoracomeres 5 and 6 (sometimes 4) humped and setose. Wedge-shaped pleural sclerites present. Limbs 2–5 with pairs of seminal receptacles. Telsonic spines present.

Material.—Holotype ♀ (USNM 191138), 8 paratypes (5 ♀♀, 2 young ♀♀, 1 ♂) (USNM 191139), on *Chrysogorgia* sp. (USNM 49895); ALBATROSS sta. 5621 (28-XI-1909; between Halmahera and Makyan Islands, Indonesia, 0°15'00"S, 127°24'35"E; 554 m).

Relationship to Host.—Carapace covered by thin coenenchyme layer except for posteroventral aperture. Host axis encompassed by, and sometimes overgrowing, anteroventral protrusions of mature female carapaces.

Etymology.—A noun in apposition, with a latinized ending, from the Spanish, named for a fancied resemblance of the carapace to helmets worn by Spanish conquerors of the New World.

Description of Females.—Holotype 2.7 mm long and wide, 2.5 mm high; 3 mature paratypes respectively 2.8 mm long and high, 2.4 mm long and 2.0 mm high, and 3.0 mm long, 2.8 mm high, 2.4 mm wide. Overall appearance helmet-like (Fig. 3A, B). Dorsal half of carapace produced into a three-quarters elliptical crest and pair of hemispherical lateral protrusions. Pair of curved, anteroventral projections (anchor). Posteroventral corner compressed, with slit-like, vertical opening into brood chamber. Ventral margins of valves discernible as longitudinal seam. External surface pierced by innumerable pores; grapnel-like projections concentrated ventrolaterally and on anchor. Gut diverticulum in each half of carapace has bifurcate ventral branch and several short dorsal branches that do not extend out into crest.

Subadult females with smaller, less highly chitinized carapaces, mostly due to weaker development of dorsal crest and lateral protrusions. Typical size 1.9 mm long, 1.6 mm high, 1.2 mm wide. Anteroventral protrusions short, pointed, not reaching around host axis.

Main body (Fig. 3C) occupies ventral half of carapace. Antennules little more than half as long as oral cone when folded, about as long as it when extended. Minute antenna found in only one specimen, likely overlooked in others. Each thoracomere with pair of thoracopods not reaching as far ventrally as oral cone; dorsum slants downward posteriorly, so first segment highest, others progressively less tall. First segment has moderately tall, upright protuberance covered with fine hairs; second may have much shorter, naked protuberance; thoracomeres 5 and 6 (sometimes 4) have low, setose, dorsal humps. In immature female dorsal protuberance of thoracomere 1 very small, only sixth segment humped. Ventral edges of thoracic tergites well marked, sixth inflated into large, lateral epaulets; wedge-shaped sclerites in pleural region of thoracomeres 2–5. Abdominal segments rectangular, first with vestigial ventral penis, last (telson) with dorsal ctenate ridges, pair of minute posteroventral spines, and furcal rami.

In antennules (Fig. 3D) third article triangular, others rectangular, third and fourth shorter than rest, sparsely hirsute; fourth and fifth articles with 1 anterior seta each. Sixth article ends in hooked claw with seta at base and another to either side (latter 2 often difficult to discern); posterior edge with 2 short, distal processes, each with 2 setae, those on proximal process longer.

Antennae biramous (Fig. 3E), one ramus papilliform, the other finger-like.

Anterior edge of oral cone somewhat convex. Mouthparts as per generic diagnosis (Fig. 3F–I).

Thoracopods 1–5 of about equal length, sixth pair markedly shorter (Fig. 3B). Coxa of first limb tapered, twice as long as maximum width (Fig. 3J), posteriorly

directed genital pore at its base; laterodistal seta as long or longer than elongate basis. Coxa and basis lined with dense hairs. Rami equal, very long and narrow, their articles approximately equal. Coxae of limbs 2–5 (Fig. 3K) with basolateral, ear-shaped lobe; bases square; exopods thicker and more setose than endopods, first 2 articles of endopod almost fused in fifth limb. Seminal receptacles variably shaped in mature females, absent in immature ones (Fig. 3C). One receptacle of each pair may overlap into basis; sometimes only 1 receptacle in fifth limb. Ducts open separately in pleural region. Sixth limb (Fig. 3L) with reduced setation; exopod longer, thicker, and more setose than endopod, distal article of each ramus longer than proximal one. Representative setal count for mature female compiled in Table 2.

Penis almost completely reduced.

Furcal rami (Fig. 3M) about 0.3 mm long, upturned and tapered distally to $\frac{1}{3}$ basal height, covered with cuticular ctenae; posterodorsal spine and variable setation (e.g., 4 medial, 7 terminal, or 9 medial, 4 terminal); setae less than half as long as rami, with short setules.

Description of Male.—Carapace almond-shaped, 2.56 mm long, 1.38 mm high, 1.00 mm wide; anterior end with asymmetrical protuberance (Fig. 4A). Carapace bivalved (Fig. 4B), fused only from anteroventral quarter to middorsal hinge; grapnels dense along ventral edge of valves. Adductor muscle inserts on valves about $\frac{1}{3}$ posteriorly at midheight. Gut diverticulum in each valve has short anterior branch and longer posterior branch, latter giving rise to bifurcate dorsal branch and long, straight, posterior branch. Valves also contain complexly lobed testicular tissue.

Main body occupies anterior $\frac{2}{3}$ of carapace (Fig. 4C). Antennules extend much farther ventrally than oral cone; well developed antennae arise behind them. Thorax has 6 pairs of biramous, setose thoracopods reaching farther ventrally than oral cone. Dorsum almost straight; first thoracomere shorter than rest, articulation with head clear. Ventral edges of thoracic tergites well marked, forming large, flat epaulets on sixth segment. First, second, and third abdominal segments rectangular, slightly longer than high; third and fourth trapezoidal, forming bottom of U. First segment with ventral penis, fifth (telson) with pair of minute postero-ventral spines and furcal rami.

Antennules quite large (Fig. 4D). First and second articles rectangular, second larger, both unarmed. Third and fourth articles triangular, latter very short, with 2 equal, anterior setae. Fifth article as long as first and second combined, with about 25 setae opposite terminal article. Sixth article narrower and a little shorter than fifth; sharp claw at tip has short seta at base and another at either side; 2 closely spaced processes on posterior edge of article, proximal one very small with 2 long setae, distal one (claw guard) long and thick with 3 short, terminal setae.

Antennae biramous (Fig. 4C). Ventral ramus hangs alongside oral cone with row of lanceolate setae and several rounded, distal projections. Posterior ramus reaches to abdomen and tapers distally with few stubby, subterminal setae.

Oral cone short, equilaterally triangular in profile; bifurcate ends of maxillae protrude from tip. Other mouthparts not examined.

Limbs subequal in length, first 5 pairs similar to females except laterodistal coxal seta much shorter than basis in first pair and exopod in limbs 2–5 with long distal article (Fig. 4E). Sixth limb (Fig. 4F) similar to others, but protopod less setose; unique among described ascothoracids in having an apparently triarticulate endopod (normally biarticulate). Setation pattern of left thoracopods compiled in Table 2.

Table 2. Thoracopodal setal counts of *Thalassomembracis* spp. Conventions are the same as in Table 1, except that only seven positions are enumerated (Fig. 4E), and ranges are given for partly obscured positions. There are never any medial setae on the coxa or lateral setae on the basis

Species and limbs	Position on Limb						
	1	2	3	4	5	6	7
<i>T. conquistador</i> ♀							
I	1	0	4	2	(0)		0
II	1	1	10	4	1	1	1
III	1	1	8	4	1	1	1
IV	1	1	11	4	1	1	1
V	1	1	?	5	2	0	1
VI	0	0	6	2	(0)		0
<i>T. conquistador</i> ♂, left							
I	1	0	6	6	(3)		0
II	1	1	14	4	1	1	5
III	1	1	15	8	1	1	5
IV	1	1	?	6	1	1	4
V	1	1	14	6	1	2	4
VI	0	1	11-13	6	2	2	1
<i>T. tetraedus</i> ♀, I right, II-VI left							
I	1	0	2	1	(0)		?
II	1	1	8-9	4	1	1	0
III	1	1	8?	5	1	1	0
IV	1	1	8-10	?	?	?	0
V	1	1	10	6	1	0	0
VI	0	(5)		3	(0)		0
<i>T. bilobus</i> , compiled from 2 ♀♀ (ranges are actual differences, not uncertainties)							
I	1	0	4	1-2	(0)		0
II-IV	1	1	8-9	4-5	1	1	1
V	1	1	11-12	4	1	0-1	1
VI	0	0	5-6	3	(0)		0
<i>T. orientalis</i> ♀, holotype, right							
I	1	0	4	2	(1)		0
II	?	1	10	4?	1	1	2
III	1	1	10	?	1	1	2
IV	1	1	11	4	2	1	2
V	1	1	?	5?	1	1	1
VI	0	0	10	4	(1)		0
<i>T. acanthosphaericus</i> ♀, holotype, right							
I	1	0	7	3	(0)		0
II	1	1	15	7	1	1	0
III	1	1	16?	7	1	1	0
IV	1	1	16?	6?	1	1	0
V	1	1	19	7	1	1	1
VI	0	1	14	5	(1)		0
<i>T. bayeri</i> ♀, holotype, left							
I	1	0	4	3	(0)		0
II	1	1	10	3	1	1	1
III	1	1	12	4	1	1	1
IV	1	1	11	3	1	1	2
V	1	1	11	4	1	1	2
VI	0	0	8	3	(1)		0

Penis cylindrical with several short, subterminal setae and 3 longer, terminal ones (Fig. 4G).

Furcal rami 0.39 mm long, 0.12 mm high basally, tapered to $\frac{1}{3}$ as high at downturned distal end (Fig. 4H). Row of 17 long, medial setae; 5 shorter, plumose, distal setae. Medial and lateral surfaces covered with cuticular ctenae.

Progeny.—Two females were brooding oval eggs, one 63, the other 32 (mean size of latter $306 \times 243 \mu\text{m}$). A third female was brooding nauplii, 4 of which were removed for examination.

Nauplii oval, 0.45–0.46 mm long, 0.34–0.35 mm wide, with dish-like dorsal shield (Fig. 4I), naupliar appendages clustered at front end of ventral side; round, yolk-filled midgut occupies posterior half of shield. Papilliform frontal filaments anterior to small, pointed labrum. Antennules (Fig. 4J) at least biarticulate, with 2 medial setae, 3 terminal setae (2 long, 1 short, exact lengths variable), and subterminolateral seta. Antennae (Fig. 4K) biramous, protopod with spinule on gnathobasic lobe; exopod about 9-segmented, last 5 articles with long, medial seta; endopod cylindrical, triarticulate, shorter than exopod, with short medial spine on first article, long medial seta on second, and 2 long, terminal setae. Mandibles like antennae but exopod shorter, with only 4 setae. Primordia of maxillules sometimes visible under cuticle. Posterior end of body with anal spine and pair of tridentate abdominal spines, which contain rudiments of simple spines of next instar (Fig. 4L).

Remarks.—The tall thoracic protrusion in this species is reminiscent of the dorsal horn of *Gorgonolaureus* (Grygier, 1981b; c), but in that genus it is the second thoracomere which is modified, not the first, so they are probably analogous structures. The anteroventral carapace anchor is most highly developed in this species, and its grip around the host axis assures that the parasite cannot be easily dislodged.

The male has many of the characteristics of the so-called late protander of *G. muzikae* (Grygier, 1981b), rather than a true male or protander. Its carapace is not truly bivalved since there is considerable anterior valve fusion. There is a short primordium of the anchor, the antennae are but weakly armed with sensilla, and the limbs and furca have setae too short to be natatory. If *T. conquistador* is a protandric hermaphrodite like *G. muzikae* (Grygier, 1981b), this specimen has already begun to change to a female.

Thalassomembracis tetraedus new species

Figure 5

Diagnosis.—Carapace about 4 mm, tetrahedral with long anteroventral anchor, posterior end irregular and acute; external ornamentation of hooked grapnels. Antennular claw hirsute with basal and 1 lateral seta; 3–4 setae on claw guard, 2 on proximal process. Oral cone longer than deep. Thoracomeres 5 and 6 humped and setose. Wedge-shaped pleural sclerites present. Limbs 2–5 with pairs of seminal receptacles. Two setae on exopod of first limb, 1 on endopod. No telsonic spines. Dorsalmost, terminal furcal seta thicker than others.

Material.—Holotype ♀ (USNM 191140), 2 dissected paratype ♀♀ (USNM 191141), on *Chrysogorgia papillosa* Kinoshita (USNM 49974); ALBATROSS sta. 5665 (28-XII-1909; Macassar Strait, $4^{\circ}43'22''\text{S}$, $118^{\circ}53'18''\text{E}$; 744 m).

Relationship to Host.—Anteroventral anchor appressed to host axis but not embedded in it; except for posterior aperture, carapace completely covered by thin layer of host coenenchyme.

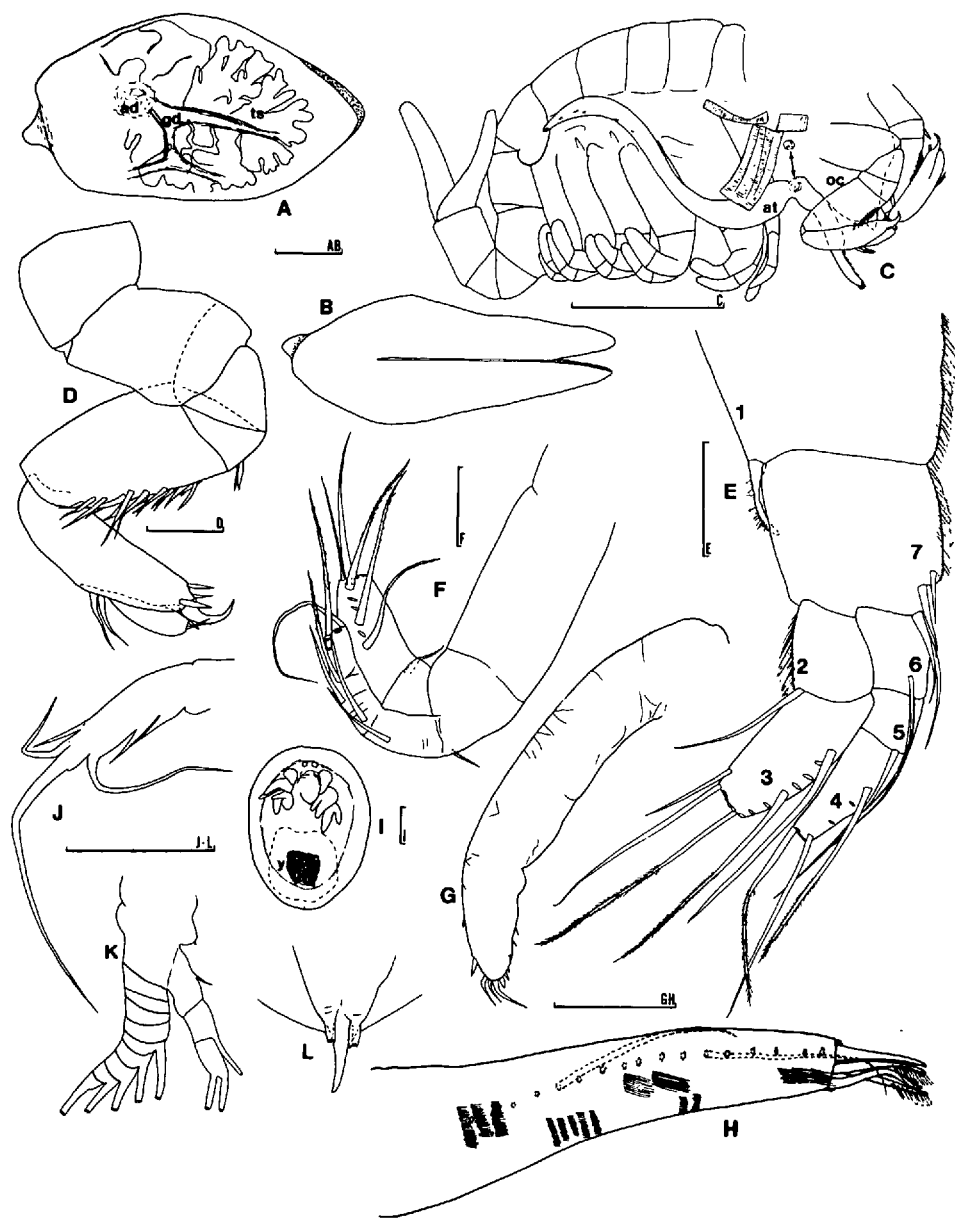


Figure 4. *Thalassomembracis conquistador* new genus and species: Paratype δ and larvae. A, B, Male, lateral and dorsal views, anterior end left; C, Main body, displacement of antenna in dissection shown by double-headed arrow, natatory setae omitted; D, Antennule; E, Distal part of third limb; F, Sixth limb; G, Penis; H, Furcal ramus, lateral view; I, Nauplius, ventral view, gut outlined by dashed line, setae omitted; J, Naupliar antennule; K, Naupliar antenna; L, Naupliar posterior spines. Not all setae and setulation shown in E, F, H, and only part of cuticular armament in H. Scales: A-C 1.0 mm, otherwise 0.1 mm. Abbreviations as in Figure 3.

Etymology.—From Greek tetra (four) and hedos (seat), referring to the 4-sided shape of the carapace.

Description.—Carapace tetrahedral (edges 4.1 mm in holotype, 3.8 mm and 4.3 mm in paratypes), anterior face steeper than posterior (Fig. 5A, B). Anteroventral anchor cylindrical; dorsolateral apices nipple-like; posteroventral apex tapered more strongly than others, irregular in side view, with short, vertical slit leading into brood chamber. Fusion seam of valves visible only ventrally. External grappels clustered posteroventrally. Midgut diverticulum in each half of carapace extends posteriorly and gives off a dichotomous ventral branch and, farther distally, a dichotomizing dorsal branch.

Main body (Fig. 5B, C) tinged dark brown, especially on thoracopods and furcal rami. Oral cone longer than deep, distal half bent slightly posteriorly, flanked anterolaterally by short antennules. Antennae not found. Anterior end of first thoracopod not well defined. Other thoracopods of equal length, their thoracopods reaching less far ventrally than oral cone, and body height less posteriorly; segments 5 and 6 with setose humps. Antero- and posteroventral margins of each thoracic tergite thickly chitinized; pair of large, inflated, lateral epaulets on sixth segment. Abdominal segments rectangular, third and fourth shorter than others; first with ventral, vestigial penis; fifth (telson) longer dorsally than ventrally, lacking posteroventral spines.

Antennules tapered except for expanded end of sixth article (Fig. 5D). First article broader than long; others rectangular, third and fourth shorter than rest, and almost fused together. Third through fifth articles with fine anterior hairs; 1 seta on fourth article, 1 or 2 basally on fifth. Curved distal claw of sixth article has hairs on convex side, seta at base, another seta laterally; 2 posterodistal processes, large rounded remnant of claw guard with 3–4 setae and numerous hairs, and smaller bump with 2 setae.

Mouthparts as per generic diagnosis (Fig. 5E–H). Tips of mandibles bifid (Fig. 5E). Distal prong of maxilla long but weak, with thin posterior flange against which movable posterior hook rests (Fig. 5H).

First limb little longer than rest, sixth markedly shorter and narrower (Fig. 5B). Basis of first thoracopod (Fig. 5I) shorter than laterodistal coxal seta; rami divided equally into 2 articles. Thoracopods 2–5 alike (Fig. 5J) with basolateral coxal lobe and 2 long, sac-like seminal receptacles in coxa, duct of each exiting in pleural region. Exopod of sixth limb unsegmented, endopod articles equal (Fig. 5K). Typical setal count, based on smaller paratype, compiled in Table 2.

Penis vestigial, essentially unarmed (Fig. 5L).

Furcal rami 0.40 mm long, 0.15 mm high at base, slightly upturned and tapered so only $\frac{1}{3}$ as high at tip (Fig. 5M). Surfaces covered with cuticular ctenae of varying lengths; 2 distal, medial setae; 6 terminal setae, thick dorsal one with expanded tip (Fig. 5M).

Progeny.—Both paratypes carried eggs dorsally within their carapaces. The larger one had 100 oval eggs, yellow with clear inclusions, averaging 0.39×0.13 mm (13 measured). The smaller paratype had 11 oval eggs 0.32×0.23 mm (all measured) and 22 naupliar embryos within the egg membrane, averaging 0.40×0.28 mm (all measured).

Remarks.—The setation of the first limb is less than the other species of the genus, in all of which besides the heavily setose *T. acanthosphaericus* new species, there are 4 setae on the exopod and 2–3 (rarely 1) on the endopod (Table 2).

Associated Fauna.—Two additional galls on the *Chrysogorgia* specimen, each



Figure 5. *Thalassomembracis tetraedus* new genus and species: Paratype ♀♀. A, Posteroventral view, anterior end down; B, Dorsolateral view, part of carapace removed to expose body; C, Thorax and abdomen; D, Antennule; E, Mandible; F, Edge of maxillule; G, Medial languette; H, Tips of maxillae, rear view; I, First limb; J, Second limb; K, Sixth limb; L, Penis; M, Furcal ramus, lateral view with detail of dorsal seta. Only typical setulation shown in I-L. Scales: A, B 1.0 mm, otherwise 0.1 mm. Abbreviations as in Figure 3.

formed of a single distended polyp, contained pycnogonids rather than ascothoracids. These are the *Ascorhynchus* sp. B of Stock (1953), which were encysted in *C. papillosa* from the same Albatross station. Judging from Stock's drawings, he examined different pycnogonid galls than those I found.

***Thalassomembracis bilobus* new species**

Figure 6

Diagnosis.—Carapace about 3 mm, dorsally bilobed, somewhat heart-shaped; ventral edges of valves free; short anteroventral anchor; posterior end rounded; most external hooked grapnels found ventrally. Antennular claw hirsute with 3 basal setae; 3 setae on claw guard, 2 on proximal process. Oral cone equilaterally triangular. Thoracomeres 5 and 6 (sometimes also 3 and 4) humped; all humped segments and first thoracomere setose. Wedge-shaped pleural sclerites present. Dorsalmost terminal seta of furcal ramus thicker than others; pores on lateral face of ramus.

Material.—Holotype ♀ with eggs (USNM 191136), 7 paratype ♀♀, at least 2 with eggs (USNM 191137) on *Chrysogorgia* sp. cf. *papillosa* (USNM 25387); ALBATROSS sta. 4187 (13-VIII-1902; 12.2 km NE of Hanamaulu, Kauai, Hawaiian Islands; 945–1,308 m).

Relationship to Host.—Carapace anchor appressed to, but not overgrown by, host axis; entire carapace, except posteroventral aperture, covered by thin layer of host coenenchyme.

Etymology.—Named for the dorsally bilobed carapace.

Description.—Holotype 3.2 mm long, 2.8 mm wide and high; one paratype 3.0 × 2.7 × 2.7 mm; other specimens similar. Carapace expanded dorsolaterally into pair of hemispheres with saddle-like depression between, outline cardioid in ventral view (Fig. 6A, B). Anchor sometimes expanded distally. Posteroventral slit-like opening into brood chamber flanked by pair of low mounds (Fig. 6C). Ventral valve margins adjoining but not coalesced, this region and anchor densely set with grapnel-like spines (Fig. 6C). Grapnels hollow with pore on top, usually with 3–8 sharp hooks radiating from top of column (Fig. 6D). Gut diverticulum in each half of carapace with posterior and dorsal branches, latter with dichotomous, anterior side branch. Ovaries between gut diverticula and outer lamella of carapace.

Main body occupies ventral half of carapace (Fig. 6A, E). Antennule about 1/3 as long as oral cone when folded. Antennae not found. Thoracopods reach less far ventrally than oral cone. First thoracomere clearly delimited from head, dome-like with pair of setose, dorsolateral ridges. Thoracomeres 2–6 about equal sized, last 2–4 (variable) humped with tuft of setae. Antero- and posteroventral margins of tergites 2–5 strongly chitinized, with large, inflated epaulets on sixth thoracomere. Abdominal segments rectangular, first and fifth longest, third and fourth shortest, posteroventral telsonic spines minute.

In evenly tapered antennules (Fig. 6F), first article triangular; second and fifth oblong and equal; third and fourth much shorter. Sparse cuticular ctenae on first 5 articles (heaviest on fourth); 1 anterior seta on fourth and fifth articles. Sixth article half as long as fifth; slender, lightly curved, distal claw has short hairs along convex side, short seta at base, and another to either side; 2 low bumps behind claw, proximal one with 2 setae, distal one (vestigial claw guard) with 3.

Mouthparts as per generic diagnosis (Fig. 6G–K). File-like row of chitinous

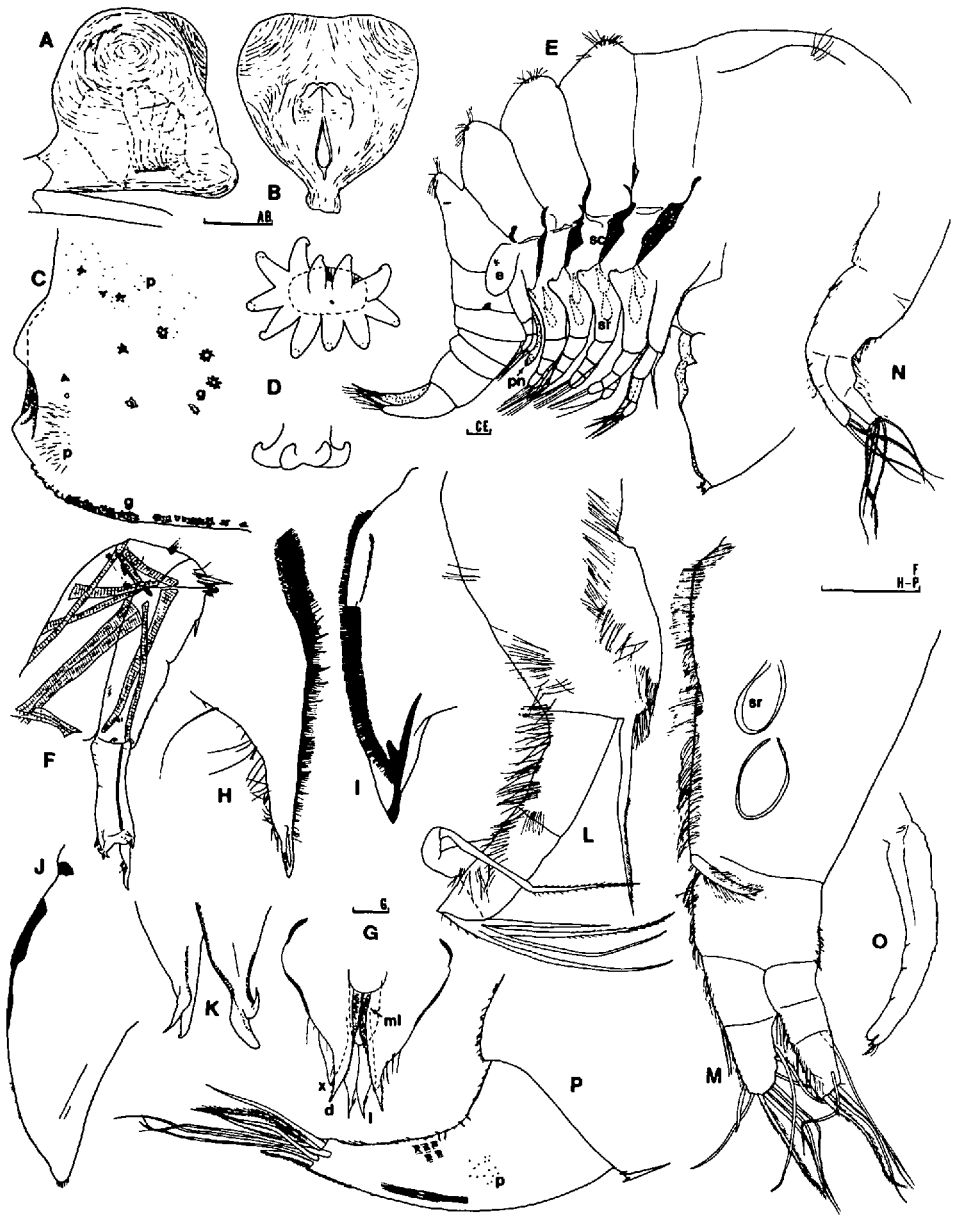


Figure 6. *Thalassomembracis bilobus* new genus and species: Paratype ♀♀. A, In situ on gorgonian, lateral view, main body outlined; B, Posteroventral view, showing gape of valve edges; C, Detail of posteroventral corner of carapace; D, Details of cuticular grapnels; E, Main body, antennules omitted; F, Antennule, first article missing; G, Mouthparts removed from labrum, anterior view; H, Mandible; I, Maxillule; J, Medial languette; K, Tips of maxillae, rear view; L, First limb, distorted; M, Fourth limb; N, Sixth limb; O, Penis; P, Furcal ramus, medial view. Only typical setulation shown in L, M, N, P, and only part of cuticular armament in P. Scales: A, B 1.0 mm, otherwise 0.1 mm. Abbreviations as in Figure 3.

teeth on tip of mandible (Fig. 6G). Basal third of anterior edge of maxillule a thin membrane lined with hairs (Fig. 6H).

First thoracopods longest, others subequal except for short, cylindrical, sixth pair (Fig. 6E). First limb lined with hairs (Fig. 6L), coxa little less than half total length of leg; basis half as wide as coxa, much shorter than laterodistal coxal seta; both rami with spinose setae, more on exopod. In limbs 2–5 (Fig. 6M) coxa longer than rest of leg, with basolateral ear-shaped lobe; laterodistal seta shorter posteriorly; articulation between first and second endopod article almost lost in limb 5. Two flask-shaped seminal receptacles in these limbs (possibly only 1 in fifth), ducts opening laterally in pleural region. Sixth limb with biarticulate rami and comparatively few setae (Fig. 6N). Setal counts abstracted from paratypes presented in Table 2.

Penis extends to middle of third abdominal segment with a few setae at tip (Fig. 6E, O).

Furcal rami (Fig. 6P) upturned and tapered, about twice as long as basal height, covered with long cuticular ctenae; short ctenae along proximal half of dorsal edge fused into denticulate plates. About 8 distal setae, a few of them perhaps arising medially, all shorter than ramus and densely setulate; ventralmost seta shortest, dorsalmost thick.

Remarks.—*T. bilobus* is the only species in the genus in which the ventral side of the carapace remains open. *T. bilobus* and *T. tetraedus* share the same species of host gorgonian, *C. papillosa*. Since they differ substantially in carapace shape, shape and armament of the telson and furcal rami, and setation of the first limb, I don't think they are simply variants of a single, host-specific species.

Associated Fauna.—At least two individuals were infested with an undescribed species of cryptoniscid isopod (Epicaridea). One had a male and a female isopod, which filled the brood chamber; another had a male amidst its brooding eggs.

Thalassomembracis orientalis new species

Figure 7

Diagnosis.—Carapace about 2 mm, laterally compressed, brood chamber not expanded very much; anteroventral depression, square posterior corner; radially toothed external papillae. Fifth antennular article lacking setae; sixth with naked claw, basal and 1 lateral seta, 2 setae on claw guard, 3 proximal setae. Oral cone equilaterally triangular. Thoracomeres 2–6 humped with transverse band of setae. Wedge-shaped pleural sclerites present. First limb little shorter than second. One spindle-shaped seminal receptacle in thoracopods 2–5. No telsonic spines. Dorsalmost furcal seta thicker than rest.

Materials.—Holotype (USNM 191142) on *Chrysogorgia* sp. (USNM 49963); ALBATROSS sta. 5367 (22-II-1909; Verde Island Passage, Philippines, 13°34'37"N, 121°07'30"E; 345 m est. from chart, not sounded).

Relationship to Host.—Held in place against host by thin layer of coenenchyme covering carapace except over posteroventral aperture.

Etymology.—Refers to the Far-Eastern collection locality.

Description.—Carapace 2.17 mm long, 2.28 mm high, 1.66 mm wide (Fig. 7A–C), nearly square in side view with dorsal half slightly enlarged and rounded, elliptical in front view. Anteroventral part shallowly depressed; posteroventral slitlike opening into interior; fusion seam of valves only visible ventrally. Outer

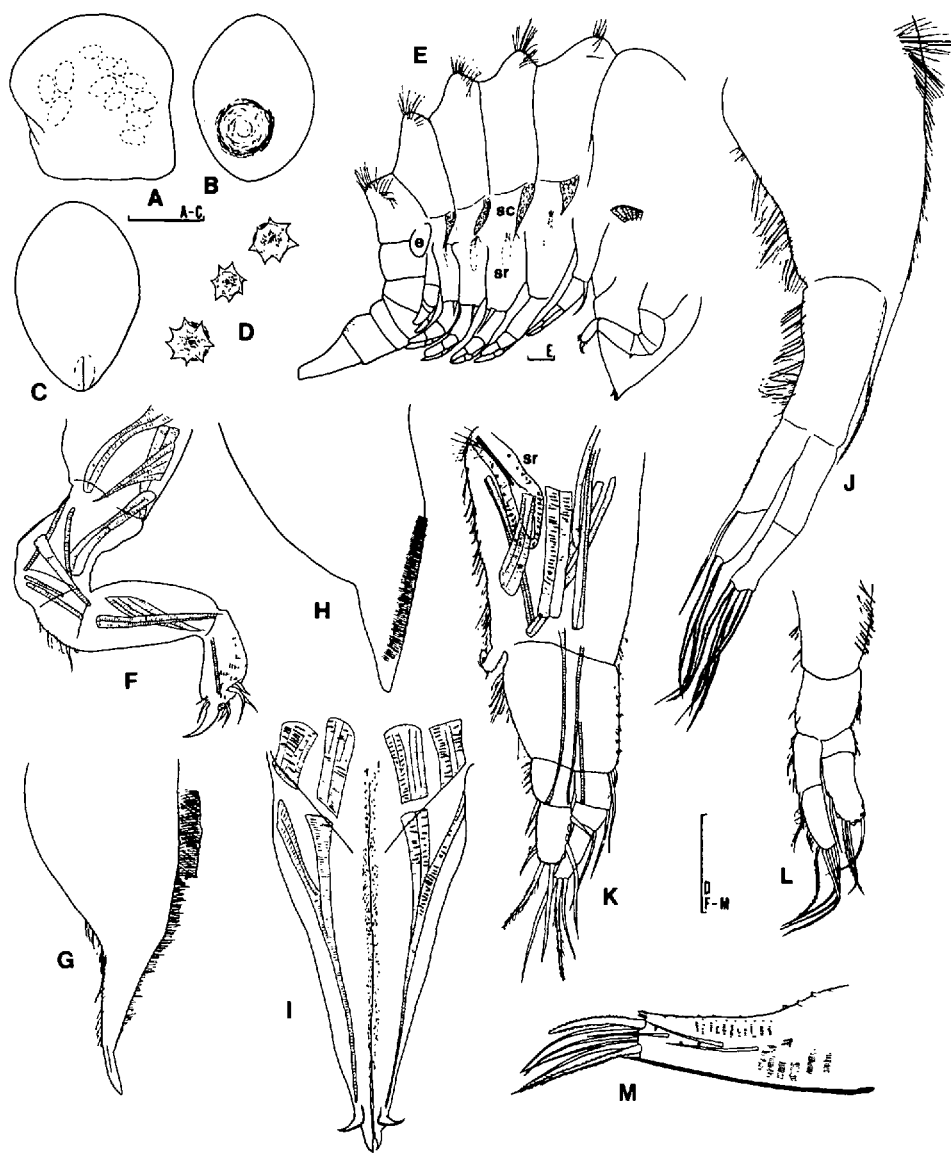


Figure 7. *Thalassomembracis orientalis* new genus and species: Holotype ♀. A, Side view with outlines of unlaidd oocytes; B, Anterior view showing depression; C, Posterior view; D, Cuticular granpels; E, Main body, natatory setae omitted; F, Antennule; G, Mandible; H, Maxillule; I, Maxillae, rear view; J, First limb; K, Fourth limb with seminal receptable; L, Sixth limb; M, Furcal ramus, medial view. Only bases of some setae shown in K, L, only typical setulation in J-M, only part of cuticular armament in M. Scales: A-C 1.0 mm, otherwise 0.1 mm. Abbreviations as in Figure 3.

cuticle with numerous, evenly spaced pores and hollow, columnar projections (Fig. 7D) 2-3 times wider than high scattered evenly half as densely as pores, each with 6-8 (rarely fewer) radial, triangular thorns and pierced by pore of greater than usual diameter.

Main body occupies ventral half of carapace (Fig. 7E). Oral cone flanked by

antennules $\frac{2}{3}$ as long as cone when folded. Antennae not found. Thoracomeres of equal length, articulation of first to head obscure, last 2 less high than others. Ventrolateral edges of tergites barely more heavily chitinized than rest of cuticle; thoracomeres 2–5 have pleural sclerites, inflated epaulets on sixth segment. Thoracopods reach almost as far ventrally as oral cone. Abdominal segments rectangular, third and fourth shorter than rest. Vestigial penis on first segment nearly disappeared; no posteroventral telsonic spines.

Articulations between second through fourth antennular articles indistinct without reference to musculature (Fig. 7F). First, second, and sixth articles about equally long, third and fourth much shorter, fifth longer than rest. Fine hairs on third and fourth articles; single seta on fourth. Few distal cuticular ctenae on fifth article. Sixth article ends in weak, basally constricted claw with small seta at base, larger one laterally; 2 weak setae on vestigial claw guard; 3 longer, thicker setae more proximally; posterior half of article covered with cuticular ctenae.

Labral sheath of oral cone thickened anteriorly. Mouthparts as per generic diagnosis (Fig. 7G–I). Row of short, distal setae along posterior edge of mandible (Fig. 7G); medial languette not seen, possibly lost in dissection.

First limb narrow (Fig. 7J), basis as long as laterodistal coxal seta; rami elongate. Coxa hirsute along both edges, basis and proximal endopod article lined medially. Second limb longest, others shorter posteriorly (Fig. 7K). Coxae of limbs 2–5 about half total length of limb, with ear-shaped, basolateral lobe. Long lateral row of hairs in these limbs, cuticular ctenae medially only on basis. Seminal receptacle and duct in each limb surrounded by thick layer of columnar cells with distal nuclei (Fig. 7K). Sixth limb shorter than others, cylindrical, lined with hairs (Fig. 7L). Endopod longer and narrower than exopod, but less setose; endopod articles equal, first exopod article very short. Setal count of right limbs compiled in Table 2.

Furcal rami 0.22 mm long, 0.11 mm high at base, tapered to half this height at squared-off distal end (Fig. 7M). Surfaces covered with cuticular ctenae, dorsal side armed with spines and denticulate plates formed from fused ctenae. Row of 6 medial setae; about 6 terminal setae, dorsalmost thicker than rest, and ventral spine. Setae about half as long as ramus, with short setules.

Remarks.—This is the only species of *Thalassomembracis* without an anteroventral carapace anchor. Nonetheless, the facies of the body is so similar to the other species that I would prefer to hypothesize a secondary loss or ontogenetic variability (as in *T. conquistador* new species), rather than propose a new genus for this species.

***Thalassomembracis acanthosphaericus* new species**

Figure 8

Diagnosis.—Carapace about 6 mm, ellipsoidal with row of spines on each side of midline; anteroventral anchor short; posterior end acute; scattered external papillae with pair of spines or 1–4 hooks. Sixth antennular article with hirsute claw, 3 basal setae, 2 setae on claw guard, 2 on proximal process. Oral cone longer than deep. Posterior maxillary hooks small. Thoracomeres 2–5 humped, sixth with transverse row of setae, fourth and fifth similar, but gap in middle of setal row. No pleural sclerites. Exopods of limbs with more terminal setae than other species: more than 5, more than 12, and more than 10 on limbs 1, 2–5, and 6, respectively. Telsonic spines present.

Material.—Holotype (USNM 191143) on *Chrysogorgia* sp. cf. *elegans*, same specimen as host of paratype of *Isidascus longispinatus*, described above.



Figure 8. *Thalassomembracis acanthosphaericus* new genus and species; Holotype ♀ and larva. A, In situ on gorgonian, lateral view with gut diverticulum dotted in; B, In situ, dorsal view; C, Details of external cuticular armament of carapace; D, Main body attached to anteroventral corner of carapace, natatory setae omitted; E, Antennule, first article missing; F, Mandible; G, Maxillule; H, Medial languette; I, Maxillae, rear view; J, First limb; K, Third limb; L, Sixth limb; M, Detail of thoracopodal seta, showing setules omitted in J-L; N, Penis; O, Furcal ramus, lateral view; P, Naupliar labrum and appendages, rear view. Scales: A, B 1.0 mm, E, P 0.1 mm, otherwise 0.5 mm. Abbreviations as in Figure 3.

Relationship to Host.—Anteroventral carapace anchor broadened distally and overgrown by host axis, so carapace held at slight angle away from axis; entire carapace except posteroventral aperture covered by thin layer of coenenchyme.

Etymology.—From Greek *akantha* (thorn) and *sphaira* (sphere), referring to the spines on the round carapace.

Description.—Carapace 6.2 mm long, 6.4 mm high, 4.8 mm wide (Fig. 8A, B). Ellipsoidal brood chamber has about 10 conical, sharp or blunt projections in 2 rows well separated from midline. Posteroventral, slitlike opening into brood chamber. Outer cuticle with innumerable pores; small, sparse papillae bearing pair of 80- μ m-long spines; and numerous grapnels with 1–4 hooks (usually 2 or 4) (Fig. 8C). Gut diverticulum in each side of carapace goes dorsally a short distance, then divides into 2 main dorsal trunks from which subsidiary branches radiate more or less dichotomously (Fig. 8A). Oocytes and yolk tissue restricted to ventral third of carapace.

Main body within ventral half of carapace (Fig. 8D). Large oral cone flanked by antennules less than $\frac{1}{3}$ as long as cone when folded. Antennae not found. Thoracopods reach little farther ventrally than oral cone. First thoracopod longer than others, articulation with head obscure; other 5 of equal length, but less high posteriorly as body bends downward. Pair of large, inflated epaulets on sixth segment. Segmental boundaries recessed in pleural region. Abdominal segments rectangular, third and fourth shorter than others, causing posterior bend.

Antennular articles oblong except for short, triangular third and fourth articles (Fig. 8E). First, second, and fifth articles equally long, fifth narrowest. Anterior hairs on third, fourth, and proximal part of fifth articles, single seta on fourth and fifth. Sixth article shorter than fifth, slightly expanded distally; distal claw with fine hairs along convex edge, flanked by short seta on each side and by seta and spinule at base; proximal process very low with 2 medium-long setae, distal one (claw guard) larger with 2 short setae.

Oral cone an isosceles triangle in profile, 50% longer than deep, with basolateral bulges. Mouthparts as per generic diagnosis (Fig. 8F–I). Posterior edge of mandible with numerous, more or less equal, fine setae (Fig. 8F). Thin, speckled membrane with short hairs along proximal quarter of anterior edge of maxillule (Fig. 8G).

Thoracopods very hirsute along entire lateral margin (not coxa in sixth pair), some mediobasal hairs. First and second limbs same length, others progressively shorter (Fig. 8D). Basis of first limb (Fig. 8J) oblong, longer than laterodistal coxal seta; rami elongate, endopod longer than exopod because of long second article, but exopod more setose. Tapering of second limb more pronounced than in next 3 pairs. In limbs 2–5 (Fig. 8K) coxa about same length as rest of limb, with small laterodistal seta and small, ear-shaped, basolateral lobe. Pair of seminal receptacles round or bottle-shaped, only 1 visible in fifth limb; narrow ducts lead to pleural region. Sixth thoracopods similar to others (Fig. 8L) except for reduced setation and equal, biarticulate rami; terminal exopod setae in double row. Setal count of right limbs compiled in Table 2.

Penis minute, conical, with 2 distal hairs (Fig. 8N).

Furcal rami 0.55 mm long, 0.35 mm high at base, $\frac{1}{4}$ as high at tip (Fig. 8O), densely clothed in long, cuticular ctenae.

Larvae.—Hundreds of immature nauplii (Fig. 8P) in brood chamber held together in bilaterally symmetrical mass by clear, viscous fluid, number estimated volumetrically at over 500. Bodies spheroidal, filled with large, round yolk and oil

droplets, averaging 0.34 mm long, 0.27 mm wide and high (16 measured). No nauplius eye or frontal filaments seen. Labrum small, pointed. Naupliar appendages unsegmented. Antennules smallest with 6 setae: 2 terminal, 2 subterminal lateral and medial, 2 medial. Antennae and mandibles biramous, exopods longer than endopods, with gnathobasic spinule on coxa and basis; row of 5 setae on antennal exopod, 3 on endopod (2 terminal, 1 medial); mandibles similar but smaller, only 4 exopod setae. Large medial spine on end of body.

Remarks.—All the other species in this genus have 2–4 terminal setae on the exopod of the first limb, 8–12 on the exopods of limbs 2–5, and 5–10 on the exopod of the sixth limb. The higher number of setae in *T. acanthosphaericus* may be due simply to its greater size. Smaller individuals might be expected to have setal counts more like those of the other species, in which case the present high counts could not be used as diagnostic criteria. However, when several adults have been available for comparison in other species (*T. bilobus*, *conquistador*, *tetraedus*), they have all been about the same size.

Associated Fauna.—Since the same gorgonian specimen was parasitized by one of the paratypes of *Isidascus longispinatus* new genus and species, there must be a lack of rigid host specificity among some of the gorgonian-inhabiting ascothoracids.

Thalassomembracis bayeri new species

Figure 9

Diagnosis.—Carapace about 3.5 mm, globular, with anteroventral anchor and square posterior corner; evenly spaced, radially toothed papillae over surface. Sixth antennular article with naked claw, 1 basal seta, 2 setae on claw guard, 3 on proximal process. Oral cone equilaterally triangular. Posterior maxillary hooks larger than distal points. Thoracomeres 2–6 humped with transverse rows of setae, patch of setae on first segment. No pleural sclerites. Thoracomeres 2–5 with single, dumbbell-shaped seminal receptacle perpendicular to body wall above each limb. In first limb, proximal endopod article longer than distal one. Telsonic spines present.

Material.—Holotype (USNM 191135) on *Chrysogorgia desbonhi* Duchassaing & Michelotti (USNM 52834); GERDA sta. 898 (10-IX-1967; west edge of Yucatan Channel, 21°04'N, 86°19'W; 240–365 m).

Relationship to Host.—Presumably attached to host axis by anteroventral anchor (not seen in situ); covered, except for posterior aperture, with thin coenenchyme and 3 polyps (Fig. 9A).

Etymology.—Named in honor of Dr. Frederick M. Bayer (USNM) who first noticed ascothoracids on gorgonians (Bayer 1956), and who conscientiously culled these parasites for eventual study.

Description.—Carapace nearly globose (3.8 mm long, 3.6 mm high, 3.2 mm wide), with short, broken-off anchor (Fig. 9A, B). Vertical, posteroventral aperture leads into brood chamber; fusion seam of carapace valves visible only along posterior $\frac{2}{3}$ of ventral side (Fig. 9B). Perforate papillae 20–40 μ m across with 4–11 short, sharp, radially directed teeth (Fig. 9C). Midgut diverticulum in each half of carapace divides into 5 main dorsal trunks, each with a few dichotomous branches. About 260 subspherical, yellow eggs averaging 0.30×0.27 mm (29 measured) in dorsal brood chamber.

Main body occupies ventral half of carapace (Fig. 9A, D). Oral cone flanked

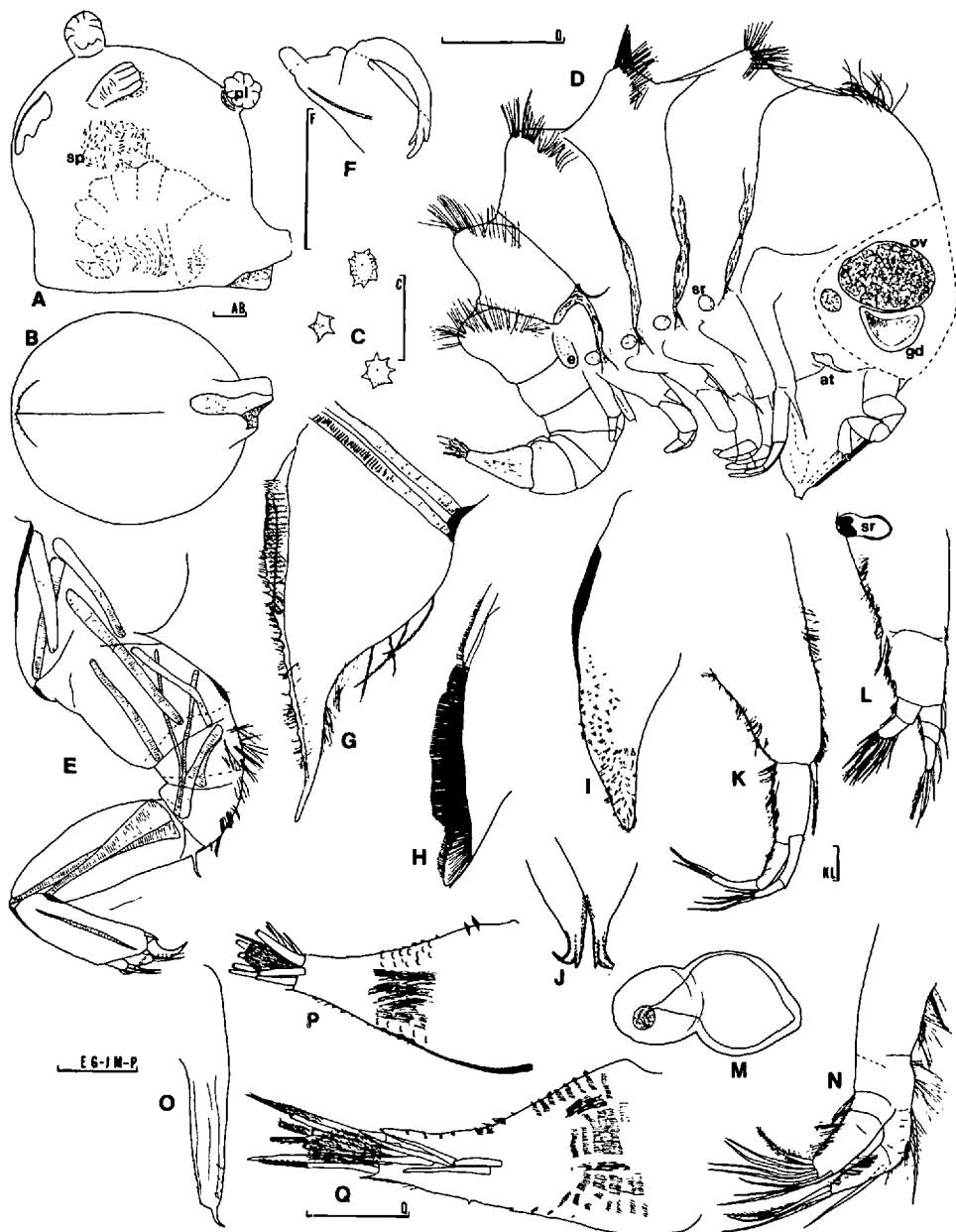


Figure 9. *Thalassomembracis bayeri* new genus and species: Holotype ♀. A, Entire animal covered by gorgonian tissue and 3 polyps, lateral view with outline of main body dotted in; B, Ventral view, anterior end right; C, Cuticular grappels; D, Main body, thoracopodal setae omitted; E, Antennule; F, Antenna; G, Mandible; H, Edge of maxillule; I, Medial languette; J, Tips of maxillae, front view; K, First limb; L, Fifth limb; M, Seminal receptacle; N, Sixth limb; O, Penis; P, Q, Furcal rami, lateral and medial views respectively. Only typical setulation shown in K, L, N, P, Q, and only part of cuticular armament in P, Q. Scales: A, B, D 0.5 mm; otherwise 0.1 mm. Abbreviations as in Figure 3.

dorsolaterally by antennae and anterolaterally by antennules that extend, when folded, $\frac{2}{3}$ as long as cone. First thoracomere longer than rest, articulation with head obscure; segments 2–4 more than twice as high as long, fifth and sixth much less high, causing body to bend ventrally. Lateral segmental boundaries in deep furrows, only fourth tergite with partial ventrolateral thickening. Medium-sized, inflated epaulets on sixth thoracomere. First 2 abdominal segments short and cylindrical, first with ventral penis. Next 2 segments narrow trapezoids causing posterior bend. Telson with ctenate dorsal ridges and small posteroventral spines.

Third and fourth antennular articles short with anterior hairs, anterodistal seta on fourth (Fig. 9E). Fifth article with anterobasal seta. Sixth article shorter and narrower than fifth, with 3 distal appurtenances: short process with 2 terminal and 1 subterminal seta; longer process (claw guard) with 2 terminal setae; sharp, movable claw twice as long as claw guard, with 1 seta at base.

Vestigial antennae biramous (Fig. 9F); anterior ramus longer and thinner than protopod, with few terminal, finger-like lobes; posterior ramus papilliform.

Mouthparts as per generic diagnosis (Fig. 9G–J). Thin speckled membrane lined with short hairs along basal third of anterior edge of maxillule (Fig. 9H). Medial languette with more cuticular ctenae than other species (Fig. 9I). Maxillae with short distal prongs and much larger posterior hooks (Fig. 9J).

First thoracopod longest, rest progressively shorter (Fig. 9D). Coxa of first limb long and narrow (Fig. 9K); elongate basis as long as laterodistal coxal seta; both edges of coxa and medial edge of basis hirsute; terminal exopod article half as long as proximal one. Limbs 2–5 constructed alike (Fig. 9L). Entire limb lined with fine hairs. Coxa tapered, especially in second pair; basolateral edge produced into narrow flap overlapping following limb; laterodistal seta small. Dumbbell-shaped seminal receptacles (Fig. 9D, M) about 0.14 mm long, 0.07 mm wide; internal, thick-walled reservoir opens externally through duct piercing very thick, chitinous plug. Sixth pair of limbs (Fig. 9N) with coxa twice as long as wide, square basis, exopod with very short basal article. Setal count of left thoracopods compiled in Table 2.

Penis 0.25 mm long, with distal seta (Fig. 9O).

Furcal rami 0.29 mm long, 0.17 mm high at base, tapered distally (Fig. 9P, Q). Entire surface with cuticular ctenae, fused into short, denticulate scales near margins, free and much larger on faces. Few small spines along ventral edge, larger one at distal corner. Row of about 8 medial setae starts near midlength; about 5 distal setae; setae about half as long as ramus, with numerous, very short setules. Oval, fuzzy object nestled amidst distal setae, obscuring them (uncertain if this is modified seta or foreign object, but found on both rami).

Remarks.—*T. bayeri* has seminal receptacles of a form unique in the Ascothoracida, and it is the only species of *Thalassomembracis* lacking both the medial and lateral, claw-flanking, antennular setae. What is its relationship to the other species in the genus? *T. bayeri* and *T. orientalis* both have a posteroventrally square carapace with radially spiny grappels instead of hooked ones, a single seminal receptacle per limb, a hairy antennular claw (also in *T. tetraedus*), and dorsal thoracic setae in rows (also in *T. acanthosphaericus*). Most of these conditions cannot be judged primitive or derived by comparison with *Synagoga*, *Gorgonolaureus*, and *Isidascus*, some subset of which must be the sister group of *Thalassomembracis*. The hairy claw is derived and perhaps synapomorphic, but otherwise these other genera have none of the character states in question (cf. above, Moyse, 1983; Grygier, 1981b; c; 1983c), so a hypothesis of close phylo-

genetic relationship between *T. bayeri* and *T. orientalis* is only weakly substantiated.

On the other hand, *T. orientalis* and the other Pacific species (*T. tetraedus*, *conquistador*, *bilobus*) all have large pleural sclerites. All but *T. conquistador* also have a thick, dorsal furcal seta, and *T. orientalis* and *T. tetraedus* have but one claw-flanking seta and no telsonic spines. All four of these character states seem to be apomorphic by comparison with the three out-group genera; their concordance suggests that the Pacific species are a monophyletic assemblage, the sister group of *T. bayeri* and/or *T. acanthosphaericus* in the Caribbean region. Since it is not possible to demonstrate a close relationship of the latter two species, *T. bayeri* may be quite isolated within *Thalassomembracis*. If *T. bayeri* is distinct phylogenetically from the other species, it may deserve subgeneric status, but the evidence is not compelling. No characters, besides the polarity-estimable ones listed above, corroborate the unity of the Pacific quartet.

DISCUSSION

Gorgonolaureus, *Thalassomembracis*, and *Isidascus* are all bathyal parasites of gorgonians and have several advanced morphological features in common (relative to *Synagoga*). All have an essentially univalved carapace with a postero-ventral aperture of varying length. They are attached to their hosts by elaborations of the front of the carapace (especially notable in *I. longispinatus* and *T. conquistador*, which encircle the host axis). The antennules are small in the adults, the mandibles and maxillules armed similarly in each genus, and the thorax has humps or horns in all species. The nauplii of *T. conquistador*, *T. acanthosphaericus*, both *Gorgonolaureus* species (Grygier, 1981b; c), and *I. longispinatus* are very much alike in having a disc-like dorsal shield, small or absent frontal filaments, and extremely weak or absent gnathobases. They differ from laurid nauplii, which are pear-shaped, lack a dorsal shield, and have prominent frontal filaments and strong gnathobases (Lacaze-Duthiers, 1883; Knipowitsch, 1892; Yosii, 1931). Laurid nauplii are clearly capable of an independent existence, while the simpler nauplii of the gorgonian parasites are retained in the brood chamber until a later, unknown stage.

It is tempting to propose a new family of Ascothoracida for these three genera, based on several adult and larval synapomorphies. This step may be taken in the future, but for now, there are two reasons to leave them in the Synagogidae. *Synagoga mira*, the type of the family, and its congener (Grygier, 1983c), are the only other ascothoracids with a medial languette that rivals the true mouthparts in size, although some petraracids have smaller ones (Grygier, 1983b). A large medial languette is clearly apomorphic, and if its distribution in the subclass is truly what it seems, it might be a synapomorphy of a more strictly defined Synagogidae. The second reason for retaining the present classification is stability. Many more ascothoracids are in the process of description (Grygier, unpublished data), and I wish to delay higher-level reclassifications until all the new forms have been treated.

ACKNOWLEDGMENTS

Drs. S. D. Cairns and F. M. Bayer kindly loaned me specimens of ascothoracid-infested gorgonians from the USNM collections, and Dr. W. A. Newman (SIO) passed on to me specimens that had been loaned to him by Dr. Bayer. I thank Dr. John Moyse (University College of Swansea) for allowing me to see page proofs of his paper on *Isidascus*. I have benefitted from discussions with Dr. Newman,

who also criticized the manuscript. This work, a Contribution of Scripps Institution of Oceanography, new series, was partly done during the tenure of an NSF graduate fellowship and was partly supported by NSF Grant DEB78-15052.

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DATE ACCEPTED: December 20, 1982.

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